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First Cretaceous Specimens of the Beryciform Fish *Hoplopteryx* from North America and Their Bearing on Acanthopterygian Evolution

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A complete price list of Pearce-Sellards papers and other bulletins and miscellaneous publications of the museum will be sent upon request.

—Jane Sullivan, Editor

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FIRST CRETACEOUS SPECIMENS OF THE BERYCIFORM FISH *HOPLOPTERYX* FROM NORTH AMERICA AND THEIR BEARING ON ACANTHOPTERYGIAN EVOLUTION

By David Bardack[1] and Susan Teller-Marshall[2]

ABSTRACT

Hoplopteryx lewesiensis (Beryciformes: Trachichthyidae) is reported from North America for the first time. More than a dozen individuals, including several complete fishes, expand the geographic range of this Late Cretaceous fish. This acanthopterygian, characterized by an unchanging morphology across a long geologic interval and broad geographic area, indicates that the epeiric seas of the northern seaway were relatively homogeneous environments. It appears also that the beryciforms as well as the perciforms developed outside of these seas.

INTRODUCTION

Hoplopteryx is one of the five Upper Cretaceous genera of trachichthyid fishes (Order Beryciformes). The beryciform fishes are generally considered to be representative of a basal group from which more advanced acanthopterygian fishes radiated during the early Tertiary. Modern trachichthyid beryciforms are mostly deepwater fishes (Zehren, 1975), but Upper Cretaceous trachichthyids are found in deposits formed in relatively shallow epeiric seas (Patterson, 1964, 1967). Both fossil and recent genera are characterized by deep, compressed bodies, a series of mucous cavities on the cranial roof, and a large, oblique mouth.

Hoplopteryx is known from Upper Cretaceous deposits in Lebanon, England, France, Germany, Czechoslovakia, and the U.S.S.R. (Patterson, 1964). The specimens described here are the first records of *Hoplopteryx* from a North American Cretaceous deposit.

The Texas material may be assigned to *Hoplopteryx lewesiensis,* the most common species of this genus. Specimens are well preserved and permit detailed examination. In almost every respect, the North American *Hoplopteryx* is indistinguishable from *H. lewesiensis* fossils known from Europe.

H. lewesiensis ranges from the Cenomanian to the Santonian stages of the Upper Cretaceous (Patterson, 1964) and is also widespread geographically. This species is morphologically stable throughout its geologic and geographic ranges, appearing suddenly (in a geological sense) with its full complement of characteristics clearly distinct from its contemporaries. This is a pattern typical of many Cretaceous fishes.

In the past few years the monophyletic nature of the beryciform fishes has been questioned by Zehren (1975) and Rosen (1973) who suggest that the beryciforms represent a structural grade in teleostean evolution. In any

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event, *Hoplopteryx lewesiensis* represents one of the more successful experimental combinations of characters, called beryciform, that appear suddenly in the Cenomanian.

ABBREVIATIONS

Abbreviations used in this text include BMNH: British Museum of Natural History, and TMM: Texas Memorial Museum.

ACKNOWLEDGMENTS

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GEOLOGY AND PALEOECOLOGY

The fossil specimens were obtained from a quarry locally called the Maness Pit. This pit was worked for road gravel in the 1930s but has been flooded for many years. It is 1.5 miles north of Roxton (about 2 miles north of the center of town) on the west side of Highway 38 in Lamar County, Texas.

According to information recorded at the time of collection, the fossil material occurred in a cross-bedded sandy limestone easily divided into two parts: the upper part thinly bedded and ferruginous with significant cross bedding, and the lower part more massive and buff colored with occasional red ferruginous streaks. The fish fossils occurred primarily in the lower part in ferruginous concretions which appeared as red balls in the massive limestone. Typical specimens are shown in figures 1 and 2.

Echols (1972) refers to these strata as the Roxton Limestone (Senonian), the uppermost unit of the Austin Group. She provides a measured section of a nearby locality. This locality (East Texas State University No. 38), ". . . just east of Texas Highway 38, 1.3 miles north of bridge on Cane Creek, north side of Roxton, Lamar County. . ." is described thusly: ". . . biomicrite, tan, weathers tan to light grey-tan, with streaks and blotches of red, maroon and yellow iron oxide stains, base gradational, lower part massive, upper part thin bedded, rest is cross bedded. . . " (p. 230).

Echols (1972, p. 45–72) presents a discussion of the lithology, paleontology, and depositional environment of the Roxton Limestone. According to her observations, the vertebrate concretions show pyrite nearest the bone with a layer of calcite-cemented hematite, followed by an outer pink discoloration of the matrix. This is surrounded by firm calcite matrix, which may form concretions. These "nodules" are not syn- or postdepositional in origin, but appear to develop later in the weathering cycle when the bones are exposed to ground water. The Roxton unit was deposited in shallow, warm water perhaps deeper than the inner neritic zone, with much plankton and nekton to serve as food sources for the vertebrates.

Among the invertebrates present are the pelecypod *Inoceramus*, the ammonites *Baculites* and *Scaphites*, as well as additional undescribed ammonites, decapod crustaceans, a rudistid mollusc, a brachiopod (*Terebratulina*) and a piece of a starfish (Echols, 1972).

SYSTEMATIC PALEONTOLOGY

Order Beryciformes, Regan, 1911

Family Trachichthyidae, Bleeker, 1859

Diagnosis. See Patterson (1964, p. 304)

Genus *HOPLOPTERYX* Agassiz

Diagnosis. See Patterson (1964, p. 305)

Hoplopteryx lewesiensis (Mantell)

For synonomy see Patterson, 1964, p. 305

(Fig. 1–5, Table 1)

Diagnosis (emended).—*Hoplopteryx* reaching about 30 cm standard length, depth of trunk equal to 48–61 percent standard length; dorsal fin with 5–6 spines and 10–11 soft rays; anal fin with 3–4 spines and 8 soft rays; longest dorsal fin spine equal in length to less than 1/3 maximum trunk depth; superficial bones of the head with coarse-ridged or spinous ornament, mucous cavities on the skull roof separated by thin crests with spiny edges; mandibular teeth expand onto lateral face of dentary near symphysis; mandibular sensory canal running in an open groove; edge of preoperculum coarsely and irregularly striated; 25 centra, 11 abdominal; caudal skeleton with 3 procurrent caudal spines above and 2 below, neural arch of PU 2 fused with centrum, first epural enlarged and oriented over neural arch of PU 2; about 11–12 scales in each transverse series, lateral line passes through 9th scale above ventral border; no ventral ridge scales.

Holotype.—Specimen in counterpart BMNH 4014, 4015.

Referred specimens.—TMM 30962-1, whole fish; TMM 30962-2, whole fish; TMM 30962-3, whole fish; TMM 30962-5, anterior half of fish; TMM 30962-10, anterior half of fish; TMM 30962-11, anterior half of fish; TMM 30962-12, whole fish; TMM 30962-13, two whole fish in one block; TMM 30962-18, anterior portion of body plus lower jaws, right opercular bones and pectoral girdle; TMM 30962-19, whole fish; TMM 30962-21, fragments; TMM 30962-22, part of vertebral column; TMM 30962-23, whole fish except for neurocranium.

Description.—*Hoplopteryx lewesiensis* was described previously by Smith-Woodward (1902) and Patterson (1964, 1968). The present account is based upon North American specimens and primarily compares and contrasts them with European material.

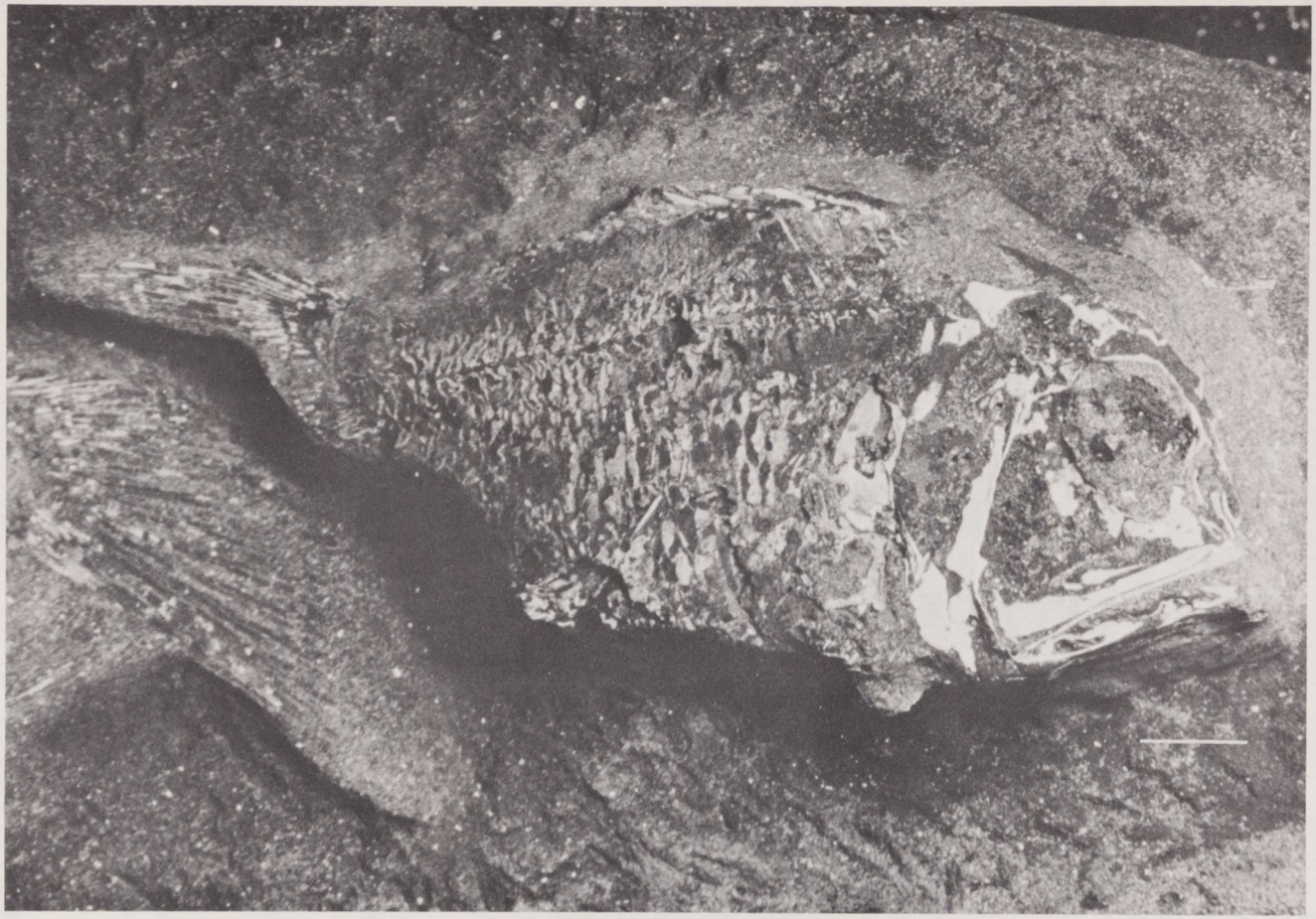

Figure 1.–*Hoplopteryx lewesiensis* TMM 30962-13 from the Roxton Limestone. Scale bar = 1 cm.

Although the number of intact, complete specimens is limited, a noteworthy feature of the group emerges from a graph of standard length versus greatest depth. The resulting points form a linear series with a constant slope (fig. 3), a pattern characteristic of growth in modern teleosts. Body measurements and fin ray counts of North American specimens are shown in table 1. All of these data demonstrate that the Texas specimens represent various growth stages of one species.

For figures of the cranial elements of European *H. lewesiensis* see Patterson (1964, p. 306–320). See figure 4 for the caudal skeleton of the Texas specimens. For figures of the caudal skeleton of European *H. lewesiensis* see Patterson (1968, p. 70–71).

Neurocranium.—The distinguishing features of the neurocranium in *Hoplopteryx lewesiensis* and the Texas specimens are the crests and depressions that form the mucous cavities and sensory canal paths on the cranial roof. The roofing bones are slightly ornamented along their crests and lateral edges with what Patterson (1964) calls short spines. Most of the neurocranial description is based upon TMM 30962-12 and TMM 30962-19, in which all but the posteroventral part of the neurocranium is preserved.

The most anterior elements of the cranial roof are the nasals—large, triangular bones sutured to the frontals. The nasals are concave in dorsal view. Anteriorly each nasal forms a tube which encloses the anterior end of the supraorbital sensory canal.

Behind the nasals are the paired frontals. At their anterior end is a transverse bridge of bone that overlays the path of the supraorbital sensory canals. The main crest on each frontal diverges as it passes posteriorly to this bony ridge, and forms the lateral wall of an expanded supratemporal fossa. Posterolaterally the frontals expand over the dorsal surface of the sphenotics. Medial to the sphenotics each frontal forms a tube which meets the anterior end of a ledge formed by the parietal. Both of these structures mark the path of the posterior segment of the supraorbital sensory canal.

Between the parietals is a large supraoccipital whose crest rises from the floor of the supratemporal fossa. This crest extends forward to the posterior edge of the orbit and attains the same height as those crests which enclose the mucous cavities.

Flanking the supraoccipital posteriorly are the epioccipitals. Each epioccipital has a posterolateral process hollowed out to form a socket for receipt of the dorsal limb of the posttemporal. The epioccipital forms most of the medial wall of the large posttemporal fossa, while the floor and lateral wall of that fossa are formed by the pterotic. Below the lateral wall of the posttemporal fossa the pterotic forms most of the hyomandibular facet. Immediately above this facet is an excavation in the dorsolateral surface of the pterotic that becomes almost tubular at its anterior end. This is the dilatator fossa. The sphenotic forms the anterior portions of the hyomandibular facet and the dilatator fossa.

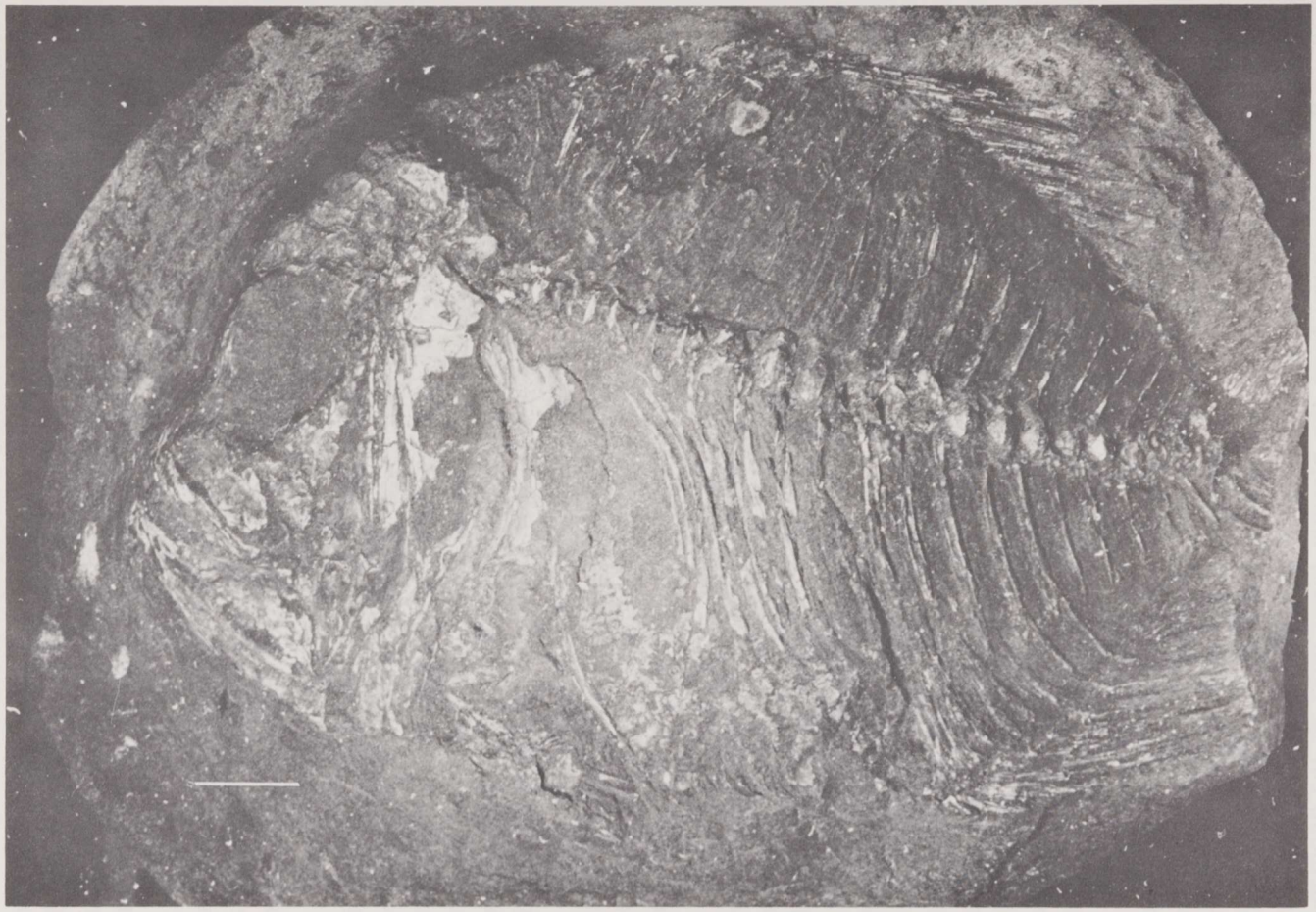

Figure 2.–*Hoplopteryx lewesiensis* TMM 30962-19 from the Roxton Limestone. Scale bar = 2 cm.

Table 1.—Measurements of the Texas specimens of *Hoplopteryx lewesiensis*. All measurements are in cm: SL=standard length; GD=greatest depth; % = percent of standard length.

Specimen Number	SL cm	GD cm	GD / SL	Pre Pectoral %	Pre Pelvic %	Pre Anal %	Pre Dorsal %
30962-1	17	10	.59	40	–	72	–
30962-2	14.3	8	.56	40	–	68	36
30962-3	18.5	10.3	.56	39	–	70	38
30962-12	21.3	11.8	.55	39	35	70	37
30962-13 left	10.5	5.5	.52	–	38	66	36
30962-13 right	8.7	4.2	.48	34	–	–	–
30962-19	21	12.8	.61	39	–	69	40
30962-23	13	7.8	.60	–	–	–	–

Beneath the sphenotics and medial to them are a pair of small pterosphenoids. In front of these is the orbitosphenoid. It extends forward into the orbital region and there is a notch in it at the exit point of the olfactory tracts.

Anterior to the orbit, the lateral ethmoids extend downward from the frontals and curve forward. Their ventral edges do not touch the parasphenoid but rather meet the vomer anteriorly.

Hyopalatine series.—The typical arrangement of hyopalatine bones occurs in *H. lewesiensis* and the Texas specimens with the hyomandibular vertical and with the pterygoids and palatine abbreviated. The medial edge of the endopterygoid does not contact the parasphenoid. The palatine exhibits a prominent maxillary process that extends dorsally from the anterior end of that bone. The quadrate is also nearly vertical, and the articular condyle is in line with the anterior edge of the hyomandibular.

Opercular series.—The bones in this series, so far as they are known in the Texas specimens, agree very well with Patterson's (1964) description of *H. lewesiensis*. All of the opercular bones have irregular edges.

The preoperculum has an oblique angle and does not broaden much about that angle. Along its anterior edge is a raised flange of bone that extends anterior to and over the preopercular sensory canal path.

The operculum, suboperculum, and interoperculum are ornamented with radiating ridges. Very little bone is preserved in this series, but TMM 30962-19 shows a characteristic strong horizontal ridge on the operculum at the point of suspension. This ridge ends posteriorly in a spine in *H. lewesiensis*, and very likely did so in the Texas specimens as well.

Infraorbital series.—These elements show a number of features which distinguish the Texas specimens as *Hoplopteryx* and *H. lewesiensis* in particular. There is a reduced antorbital plus a series of five deep infraorbitals. The latter are thickened close to the orbital edge as a bony shelf that overlies the path of the infraorbital sensory canal. Away from this thickened edge the infraorbitals are flattened and smooth, with faint ridges along their distal edges.

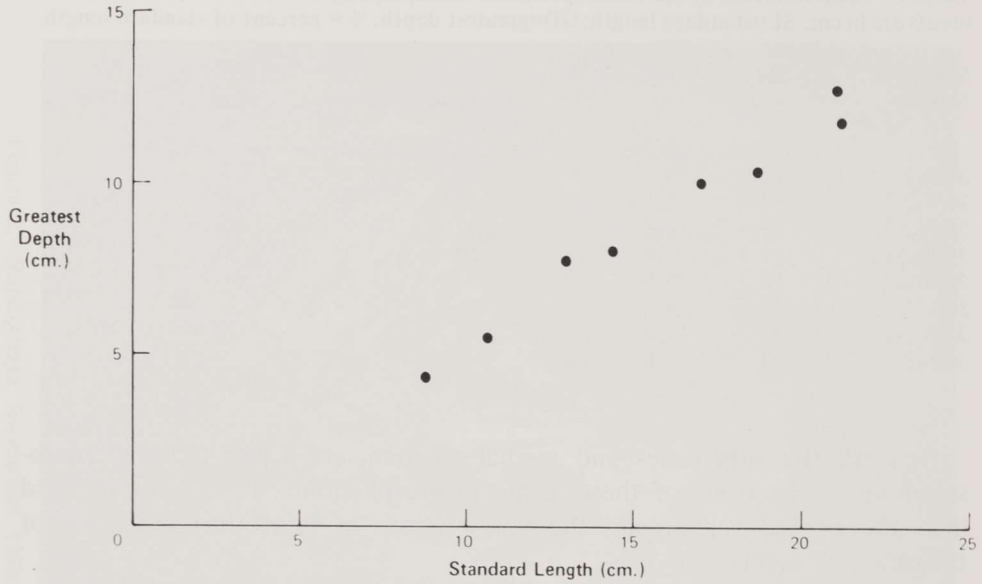

Figure 3.—Greatest depth as a function of standard length in the Texas specimens of *Hoplopteryx lewesiensis*.

The lacrimal (first infraorbital) is the largest bone in the series; it articulates anteromedially with the lateral ethmoid and palatine. A fragment of a small suborbital shelf extends medially from the dorsal edge of the third infraorbital. This shelf is preserved in TMM 30962-19.

Dermal upper jaw.—All the elements of the dermal upper jaw are identical to those described and figured by Patterson (1964, p. 315–316, fig. 51) for *H. lewesiensis*.

Mandible.—The mandible is short and deep. A characteristic feature which differentiates *H. lewesiensis* from some of the other species of *Hoplopteryx* is the extension of teeth onto the lateral face of the dentary at the lower jaw symphysis. This character is preserved in TMM 30962-2, 3, 12, 13, and 19. Aside from this feature, very little can be determined from the Texas specimens because almost no bone is preserved in the mandibles.

Vertebral column.—In *H. lewesiensis* there are 25 centra of which 11 are abdominal. TMM 30962-1 and 3 show a complete caudal count of 14 centra, and TMM 30962-12 shows a complete abdominal count of 11. The centra themselves are almost as high as they are long, with numerous bony ridges joining the thickened anterior and posterior margins.

The neural arches (except the first centrum) are fused with the centra. The last five abdominal centra have parapophyses bent down and joined in the midline, forming an abdominal haemal arch. These arches and the rib articulations with them are most clearly shown on TMM 30962-2. This character is peculiar to trachichthyoids, zeoids, berycids and various percoids (terminology of Rosen, 1973). Epipleural intermusculars are present.

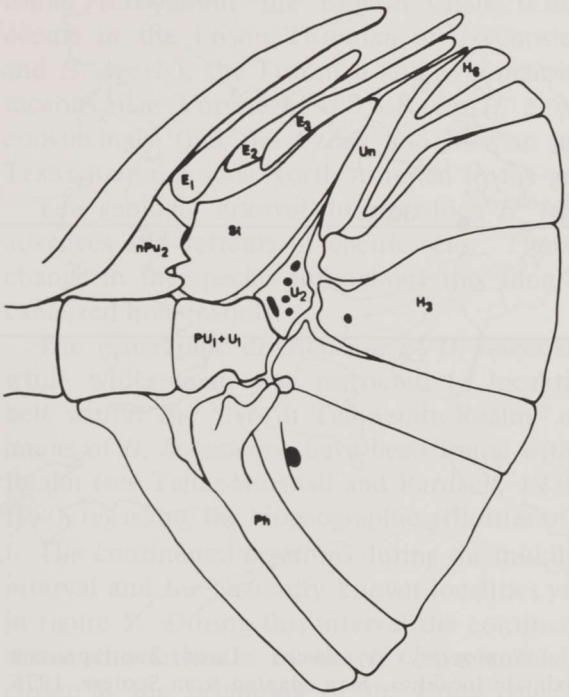

Figure 4.—Caudal skeleton of *Hoplopteryx lewesiensis*, TMM 30962-12. E=epural; NPU2=neural arch of second preural centrum; H=hypural; Ph=parhypural; PU=preural centrum; St=stegural; U=ural centrum; Un=uroneural.

Median fins.—The number of dorsal fin spines ranges from 5 to 6 in *H. lewesiensis* (Patterson, 1964); the Texas specimens have 6. As in all *H. lewesiensis* specimens with 6 dorsal spines, the dorsal soft ray count is 10. In TMM 30962-12 there appear to be auxiliary radials preceding the dorsal fin as in some European specimens of *H. lewesiensis*. Ossified middle segments exist on all the spine bearing radials except the first.

There are 4 spines and 7 soft rays in the anal fin of *H. lewesiensis* and the Texas specimens. TMM 30962-19 shows the enlarged and hook-shaped first anal radial, a characteristic feature of *H. lewesiensis*.

Paired fins and their supports.—Only fragments of the pectoral fin are preserved in the Texas specimens. The pelvic fin has one spine and 6 soft rays.

Only fragments of the pectoral girdle are preserved but the impressions left by these bones in the matrix outline the entire dermal girdle. These impressions indicate that the pectoral elements are the same relative size and shape as those figured by Patterson (1964, fig. 53). TMM 30962-19 shows the characteristic ventral postcleithrum, a long, slender curved rod of bone that extends downward to the ventral border of the trunk behind the pelvic girdle.

The pelvic girdle is also like that figured by Patterson (1964, fig. 62) for *H. lewesiensis*. Two ridges of bone radiate from a central posterior point towards the anterior end. Posteriorly an enlarged process extends medially to meet its fellow in the ventral midline. There are two pairs

Figure 5.—Geographic distribution of *Hoplopteryx lewesiensis*. Lower line represents the equator. Black dots are approximate localities. Map adapted from Scotese, 1975, and Smith et al, 1973.

of facets: a ventral pair which receive the pelvic spines and a dorsal pair for articulation of the soft rays.

Caudal Skeleton.—The caudal skeleton of the berycoids is distinctive (Patterson, 1968) and varies little within the genus *Hoplopteryx*. The caudal structure of *Hoplopteryx* is also nearly identical to that of the recent trachichthyid *Hoplostethus* (Patterson, 1968). Figure 4 shows the caudal skeleton of TMM 30962-12. The features described below are common to *H. lewesiensis* and the Texas specimens.

There is a prominent stegural plus a second uroneural. The second ural centrum is free and there are 6 hypurals. The uppermost hypural is smaller than the last of the three epurals. The first epural is elongate with an expanded proximal end that extends forward above the reduced neural arch of the second preural centrum. The haemal spine of PU 2 (and probably PU 3) is autogenous, but the neural arch of PU 2 is fused with the centrum.

TMM 30962-1 shows that the foremost caudal fin rays meet the epurals above and the haemal spines of PU 2 and PU 3 below. TMM 30962-3 shows two spines and one segmented ray in front of the lower principal rays. There are 9 dorsal and 8 ventral branched caudal rays.

DISCUSSION

Hoplopteryx lewesiensis occurs throughout the geologic range of the genus *Hoplopteryx* (Patterson, 1964) and is the only species of *Hoplopteryx* known to occur in North America and Asia, as well as Europe. Both

the geologic and geographic ranges of *H. lewesiensis* are impressive. It is found throughout the English Chalk (Cenomanian-Santonian) and also occurs in the Lower Turonian of Czechoslovakia (nominally as *H. zippei* and *H. brevis*), the Turonian and Senonian of France, and the Upper Cretaceous near Voronezh, U.S.S.R. (as *H. zippei*). Patterson (1964) argued convincingly that the Czech and Russian material is *H. lewesiensis*. The Texas material adds North America to the geographic range of this species.

The geologic interval during which *H. lewesiensis* lived was marked by advances and retreats of epeiric seas. There is little if any morphological change in the species throughout this time interval, presumably reflecting canalized homeostasis.

The geographic distribution of *H. lewesiensis* indicates that this species, while widespread, was restricted to localities along a limited latitudinal belt within the "North Temperate Realm" of Kauffman (1973). No specimens of *H. lewesiensis* have been found within the more southerly Tethyan Realm (see Teller-Marshall and Bardack, 1978; Bardack and Teller-Marshall, 1980, regarding the biogeographic affinities of the Gulf Coast).

The continental positions during the middle of the Cenomanian-Santonian interval and the currently known localities yielding *H. lewesiensis* are shown in figure 5. During this interval the continental masses were close together across the latitudes of the *H. lewesiensis* localities, and had moved still closer at the beginning of the Cretaceous (Smith et. al., 1973; Scotese, 1975). These land masses, periodically transgressed by Cretaceous seas, eventually formed a nearly continuous epeiric distributional route separated only slightly by the northern seaway. We have recently commented on the geographic and geologic stability of the Cretaceous genus *Apsopelix*, which was also apparently restricted to epeiric environments along the northern seaway (see Teller-Marshall and Bardack, 1978, pp. 29–30).

Within the genus *Hoplopteryx* there are eight described species. Three of these species are from Tethyan localities in Lebanon, and two of the Lebanon species (*H. syriacus* and *H. lewesi*) are distinctly different from the northern European species, particularly in the number of fin spines.

Hoplopteryx spinulosus from Lebanon is very similar to *H. simus* and *H. gephyrognathus* from the English Chalk. These three species differ from each other and from *H. lewesiensis* primarily in the degree of knobby ornament on the head and body. There is no directional trend within the genus relative to this ornament (Patterson, 1964, p. 337).

The seventh species, *H. macracanthus*, differs from *H. lewesiensis* only in spine length and body proportions. Patterson (1964) states that many incomplete specimens labeled *H. lewesiensis* may in fact be *H. macracanthus*. It is worth noting that Gaudant (1973) has suggested that two Cretaceous species of the trachichthyid *Acrogaster*, which differ only in minor characters and body proportions, may represent sexual dimorphism rather than distinct species. Perhaps this argument might apply also to specimens of *H. macracanthus* and *H. lewesiensis*.

Finally, there is a single specimen, *H. antiquus*, from the Turonian of Germany. It appears to differ from *H. lewesiensis* in some characters of the maxilla and dentary, but Patterson (1964) cites many similarities between the English and German species.

In summary, while there is some diversity within the genus *Hoplopteryx* from Lebanon localities within the Tethyan Realm, the more northern species of *Hoplopteryx* differ but slightly in morphology. The uniform morphological characteristics of *Hoplopteryx* throughout the Cenomanian-Santonian interval in northern seaway localities supports the belief that the epeiric sea environment was a homogeneous one.

UPPER CRETACEOUS ACANTHOPTERYGIANS

Fishes of the beryciform grade appear suddenly, in the geological sense, soon after the ctenothrissiforms disappear. Patterson (1964, 1968) argued convincingly for a close relationship between ctenothrissiforms and the beryciforms which replaced them in the Cenomanian. He believed (1967) that the beryciforms found in the Cenomanian were a group of recent origin, significant in their morphological diversity, and notable in that the character combinations in each family are mosaic in nature.

During the Turonian and Senonian, the beryciforms remained relatively unchanged in the northern seaway. As Patterson (1964) pointed out " . . . it seems certain that there was no great radiation of the acanthopterygians during this long period . . . this does not bear out the commonly held view that the teleosts, and in particular the acanthopterygians, have been radiating rapidly throughout their history." Later finds (Patterson, 1967; Gaudant, 1969, 1978a, 1978b and 1978c) have increased the diversity of Cretaceous berycoids, but these are from Tethyan localities.

Patterson's original argument (1964) was that the Cenomanian-Santonian interval showed little change. We would like to qualify that argument with the suggestion that this geologic interval showed little change in the epeiric areas of the northern seaway, but that Tethyan environments appear to have been more productive of diversity.

Patterson (1964) says "The lithology of the fish bearing deposits in the Upper Cretaceous, particularly the widespread occurrence of chalk, indicates that the Upper Cretaceous Sea was a stable habitat, unlikely to have stimulated the evolution of new forms. But the appearance of perciforms in the Danian Chalk indicates that the evolution of perciforms from beryciforms took place within this stable habitat, and that perciform evolution was not initiated by environmental upheavals at the close of the Cretaceous."

We agree that the evolution of perciforms was probably not precipitated by environmental upheavals at the close of the Cretaceous. We also agree that the Danian Chalk, like the Cenomanian-Santonian sediments, represents a stable habitat. It is not necessary to postulate that perciforms evolved in these epeiric habitats because they first appeared there. The Cretaceous localities of *H. lewesiensis* occur in a nearly continuous seaway that appears

to have been homogeneous enough to promote the wide-ranging distribution of species through time and space.

In a stable habitat it is advantageous to a species to produce few variants of significant degree. A species adapted to its environment probably has a "closed" genetic system with respect to critical variables (Carson, 1975; Gould and Eldredge, 1977). The stimulus for diversification, or rearrangement of a closed genetic system, is most likely to occur in environments marginal to or beyond the one that holds the major segment of the species population (Eldredge and Gould, 1972). Accordingly, neither the Danian Chalk nor the earlier Cenomanian-Santonian epicontinental localities appear to be likely areas of perciform evolution.

In summary, both the beryciform grade and the perciform grade are fully developed when members of these groups first appear in the fossil record. Considering the probable homogeneity of northern seaways, it is unlikely that the early evolution of these groups occurred at these localities. Where these groups developed is not known for certain, but it appears that the more southern Tethyan localities were more productive relative to acanthopterygian diversity.

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